

Life in Transition: Balancing Inertial and Viscous Forces by Planktonic Copepods

JEANNETTE YEN

*Marine Sciences Research Center, State University of New York at Stony Brook,
Stony Brook, New York 11794-5000*

Abstract. Copepods (1–10 mm aquatic crustaceans moving at 1–1000 mm s⁻¹) live at Reynolds numbers that vary over 5 orders of magnitude, from 10⁻² to 10³. Hence, they live at the interface between laminar and turbulent regimes and are subject to the physical constraints imposed by both viscous and inertial realms. At large scales, the inertially driven system enforces the dominance of physically derived fluid motion; plankton, advected by currents, adjust their life histories to the changing oceanic environment. At Kolmogorov scales, a careful interplay of evenly matched forces of biology and physics occurs. Copepods conform or deform the local physical environment for their survival, using morphological and behavioral adaptations to shift the balance in their favor. Examples of these balances and transitions are observed when copepods engage in their various survival tasks of feeding, predator avoidance, mating, and signaling. Quantitative analyses of their behavior give measures of such physical properties of their fluid medium as energy dissipation rates, molecular diffusion rates, eddy size, and eddy packaging. Understanding the micromechanics of small-scale biological-physical-chemical interactions gives insight into factors influencing large-scale dynamics of copepod distribution, patchiness, and encounter probabilities in the sea.

Introduction

Flow patterns created by solid objects moving through a fluid are influenced by viscous and inertial forces. To evaluate the relative importance of viscous and inertial momen-

tum fluxes in this solid-fluid interaction, the Reynolds number can be estimated:

$$Re = UL/v \quad (\text{Table 1, Eq. 1})$$

where U is the relative flow speed between object and fluid, L is the diameter of the object moving against the flow, and v is the kinematic viscosity (Table 1, Eq. 4).

For pelagic copepods, L varies from 10 μm for the width of a food-particle-capturing seta to 1–3 cm for the span of the antennules. These copepods exhibit movement speeds encompassing a range from less than 1 mm s⁻¹ for flow past setae to as much as 1 m s⁻¹ for escape speeds. Hence, the range of Re realms experienced by copepods spans 5 orders of magnitude, from $Re = [10^{-2}]$ to $[10^3]$. This is considered a transition zone in flow, where routine swimming and feeding take place at low Re regimes and laminar fields, whereas escapes and captures occur at high Re realms in quasi-turbulent fields. Naganuma (1996) suggests that the “flourishing dominance of the calanoids is based on the advantage of living on the border of different worlds,” the viscous and inertial. The author gives examples of activities executed by the copepod in both regimes, but does not discuss mechanisms by which the copepods derive an advantage from these physical forces. In this article, I consider how planktonic copepods make this transition to enhance the detection of chemical and fluid-mechanical signals.

Signaling in a Laminar and Quasi-Turbulent Regime

Every time a copepod moves through water, it causes a fluid deformation. If the flow is above the threshold for a mechanosensory response or contains a chemical whose concentration is above the threshold for a chemosensory response, the feature is a signal, conveying information about the propagator. Such information as size, shape, scent, speed, distance, and direction of movement are important

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E-mail: jyen@notes.cc.sunysb.edu

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Table 1

Equations to describe some biological-physical-chemical interactions of plankton

Eq. No.	Equation	Definition of terms	Source
(1)	$Re = UL/v$	Re = Reynolds number = ratio of inertial to viscous momentum flux U = relative velocity L = length of object facing flow v = kinematic viscosity	(Tennekes & Lumley, 1972)
(2)	$Pe = UL/D$	Pe = Peclet number = ratio of advection to diffusion U = relative velocity L = length D = molecular diffusivity coefficient	(Andrews, 1983)
(3)	$t_D = r_D^2/4D$	t_D = characteristic diffusion time D = molecular diffusivity coefficient r_D = characteristic diffusion length	(Dusenbery, 1992)
(4)	$v = 10^{-2} \text{ cm}^2 \text{ s}^{-1}$	v = kinematic viscosity	(Vogel, 1994)
(5)	$D = 10^{-5} \text{ cm}^2 \text{ s}^{-1}$	D = molecular diffusion coefficient for a small chemical molecule	(Jackson, 1980)
(6)	$T = (\delta^2/\varepsilon)^{1/3}$	T = eddy turnover time δ = length scale ε = energy dissipation rate	(Jiménez, 1997)

criteria for distinguishing between prey, predator, mate, host, or small-scale turbulent features. In response, the receiver will approach, retreat, orient, or continue as it was with respect to the location of the signal. One way to study signal structure is to categorize the signals by the movements that generated them.

Sinking

When a copepod sinks, no appendages are moving. Streamlines hug the body, and water beyond the body form is barely disturbed. Prey that are sinking akinetically remain undetected by mechanoreceptive predators (Kerfoot, 1978). Metabolic energy is conserved in this recovery period. While a copepod or prey item is sinking, there is little self-generated noise to interfere with the perception of the fluid-mechanical signal, so that the hydrodynamic perceptive field is at its largest. The chemical signal must be transmitted to the receptor by the slow process of diffusion.

Generating a feeding current

Movement of cephalic appendages of copepods generates feeding currents, and analyses of the feeding current reveal that it is a low Re laminar field, in which flow is orderly and streamline trajectories are predictable (Koehl and Strickler, 1981; Strickler, 1982). Each streamline projects to a specific location in three-dimensional space, and the copepod flow field serves as a map of the near-field fluid volume where each receptor receives input from signal sources at relatively defined locations. Andrews (1983) modeled the effect of the flow on the structure of the odor phycosphere, which is exuded by an algal food particle, entrained in the sheared field of the copepod feeding current. His study predicted that the shear would stretch and deform the odor field.

Within the feeding current, the Peclet number > 1 (Table 1, Eq. 2; Andrews, 1983). This Peclet value indicates that sheared diffusion is the dominant force distorting the distribution of odor, whereas Fickian diffusion has little time to act to change the structure of the odorant. The deformation separates the leading edge of the active space of the algal odor field from the alga. When the edge intersects the antennular receptor, the activated receptor gives the copepod early warning of the approach of the algal cell, allowing the copepod time to re-orient to the incoming food particle. This particle sensing and capture behavior was confirmed using high-speed cinematography (Koehl and Strickler, 1981), and the deformation of the odor field was measured using electrochemical techniques (Moore *et al.*, 1999).

In the analysis of the flow field of a freely swimming copepod, Strickler (1982) defines the field as doubly sheared: speed falls off with horizontal distance from the body axis and with distance upward from the mouthparts. Hence, receptors along the antennules and mouthparts are subject to different flow regimes. Those receptors concentrated on the mouthparts (Friedman and Strickler, 1975) receive input from a cone-like volume extending out from the copepod along the central axis of the flow field. The direction of this axis, which determines whether the flow passes over or passes by the antennular sensors en route to the mouth, can vary for different species of copepods (Strickler, 1982; Tiselius and Jonsson, 1990; Yen *et al.*, 1991; Bundy and Palfenhöfer, 1996) and can change when recognized signals elicit motor responses. Koehl and Strickler (1981) noted changes in flow orientation, which can be accompanied by changes in appendage and body orientation, in response to the odor in the alga-containing streamline of flow. Gill and Poulet (1988) note changes in the beat frequency of flow-generating appendages in response to

amino acid mixtures. At the mouthparts, flow can be fast, due to proximity to flow-generating appendages. Particles make contact with receptors nearly simultaneously with activation by the odor fields, suggesting that responses will be mediated by contact chemoreception as well as by remote detection of odors.

The paired antennules are the appendages that extend the farthest horizontally from the body. Since flow speed decreases with horizontal distance from the body axis, the antennular receptors experience a gradient in the flow. From analyses of the morphology of the sensory array, it appears that the distribution of receptors is suited to the hydrodynamic flow structure. Sensors form a linear array of putative chemical and fluid-mechanical sensors along the copepod antennules (Strickler and Bal, 1973; Chacon-Barrientos, 1980; Dourdeville, 1981; Fleminger, 1985; Yen and Nicoll, 1990; Weatherby *et al.*, 1994; Bundy and Paffenhöfer, 1996; Boxshall *et al.*, 1997; Paffenhöfer, 1998; Boxshall and Huys, 1998). Mechanoreceptors, often found evenly distributed along the antennule to a dense tuft at the distal tip, experience a gradient in flow from high speed near the proximal end to low speeds at the distal end where the tip is exposed to flow most similar to the ambient regime. The presumed use of sensors at the distal tip is for predator detection and the use of proximal sensors is for prey detection (Lenz and Yen, 1993). The results of Doall (1995) show a match between the spatial distribution of mechanosensory setae along the antennules and the three-dimensional structure of the prey-attack volume. Feathered and long setae expose large surface areas to flow and therefore should be better able to detect low speeds, whereas short stiff hairs protected in the boundary layer are gauged for high flow speeds. Having different lengths embedded in the flow allows the boundary layer to act as a flow-attenuating filter (see Weissburg, 2000, for definition of boundary layers). This is similar to the difference between superficial neuromasts and mechanosensors buried within the lateral line canal of fish (Coombs and Janssen, 1990). Furthermore, the different spacings between sensors, from the greatest distance between distal tips (which can be more than one centimeter) to the smallest separation between individual setae (on the order of micrometers) enable copepods to detect shear at the centimeter-micrometer spatial scale. According to Markl (1978), "the variability in these cuticular structures much more than differences in response characteristics of the sensory cells themselves are responsible for the large variability of mechanoreceptive function of the arthropod hairs." Since small changes in size and speed cause large changes in hydrodynamic structure at low Re —especially within the range experienced by copepods—it is essential that copepods be capable of detecting these differences with their mechanoreceptors. Such changes correspond to signals of prey, predators, mates, hosts, or small-

scale turbulence, and it is important to respond correctly to these signals.

The proximal region of the antennules is located adjacent to the flow-generating appendages, suggesting that the flow across the antennules is fast in this area. Here, we often find the highest density of chemoreceptors along the antennule (Huys and Boxshall 1998). Such high flow speeds could facilitate the detection of chemical signals by thinning boundary layers, thus shortening the time needed for the signal molecule to diffuse to the receptor (Table 1, Eq. 3). Male copepods of the species *Temora longicornis* may thin the boundary layer surrounding their receptors since they increase their swimming speed upon detecting the female odor, accelerating as they follow the mating trails. Preliminary physiological evidence indicates that copepod antennules are capable of detecting odorants such as amino acids (Yen *et al.*, 1998). In several species, differences in the structure of the female and male antennular setation (Griffiths and Frost, 1976; Fleminger, 1985; Hallberg *et al.*, 1992; Boxshall *et al.*, 1997; Boxshall and Huys, 1998) suggest that males rely more on chemosensory cues than do females. In *Euchaeta* (Boxshall *et al.*, 1997), the male, when molting into the final reproductive stage, acquires a second set of aesthetascs in exchange for its mechanoreceptive prey detection setae in the proximal region. The simultaneous loss of feeding mouthparts indicates the importance of these new sensors for mate detection. In some members of the Eucalanidae, doubled aesthetascs are present along almost the entire length of the male antennules; in other calanoid families, such aesthetascs, when present, are restricted to the proximal part of the antennule (Boxshall and Huys, 1998). Since the diffusion time through the boundary layer (Table 1, Eq. 3) is a rate-limiting step in odor perception, placement of the mate detection chemoreceptive setae within the proximal high flow zone maximizes the efficiency of odor detection. Under these physical constraints, efficient mate detection is probably one of the strongest selection pressures requiring this morphology. However, although the morphology strongly suggests an adaptive response to a surrounding flow gradient, the role of the antennule in detecting chemical signals specifically carried by the feeding currents of freely swimming copepods has not yet been experimentally demonstrated.

The forces of biology and physics are evenly matched at the scale of copepods. Given the importance of the feeding current as a sensory field, it is advantageous for the copepod to maintain this fluid structure. Analyses of the strength of the biologically generated flow in the feeding current and that of the physically derived flow of small-scale turbulence suggest the hypothesis that a careful interplay of evenly matched forces of biology and physics occurs at the scale of copepods. Under most circumstances, biological forces dominate, since turbulent length scales rarely extend to the scale of copepods (η is greater than 1 mm for near-surface

breaking waves, and ranges to 10 cm in a stratified water column (Sanford, 1997)). In the most energetic regions of the water column, the Kolmogorov flow speeds can be equivalent to the feeding-current speeds (Fields and Yen, 1997). However, these flow speeds are the average of the fluctuating component of turbulence. There will be the rogue wave of small-scale turbulence that disrupts the sensory field of a copepod. However, shear is strongly intermittent (Karp-Boss *et al.*, 1996). The energy from small-scale turbulence is at the dissipative range of fluid motion, whereas energy for feeding currents is continuously fueled by metabolic resources of the copepod. The feeding current may actually contribute energy at the lower end of the physical energy cascade. Yamazaki and Squires (1996) found that copepod swimming speeds are larger than velocity fluctuations in the seasonal thermocline and conclude that organism motion can be independent of local turbulent fields. Hence, a feeding current may momentarily be eroded by small-scale turbulence, but the biologically generated feature can be rebuilt.

At the scale of a copepod, biologically derived fluid motion is equal to and can be "stronger" than or dominant over physically derived fluid motion in its ability to deform the local fluid environment to generate a feeding current. In the face of the intruding external turbulent regime, the familiar territory of its sensory field is maintained. Within their sensory field, copepods can enhance their capability for signal detection by the coordination of flow direction and the location of sensory receptors. Water-borne signals are entrained from a complex realm of small-scale turbulence into the simpler grid-like structure of the copepod feeding current. Hydrodynamic noise is reduced within the low Re flow, further enhancing signal detection. By creating the laminar orderly structure of the feeding current, a copepod can assess the fine-scale distribution of chemicals entrained from the somewhat chaotic structure of small-scale turbulence. Information from a three-dimensional space is collapsed onto a two-dimensional external sensory array—the paired antennules—or onto the point sensor of the mouth. The copepod uses the fluid environment to accomplish much information processing externally, leaving the few hundred sensors and several hundred brain cells with a limited number of responses. The laminar flow of the feeding current simplifies the local environment and reduces the complexity of three-dimensional information processing, thus enhancing the detection of water-borne signals.

Cruising

In the cruising mode, the copepod moves ahead into the water that it pulls in towards its mouthparts. The antennular sensors project into flow not yet disturbed by the copepod's movements, thus maximizing the signal-to-noise ratio. With little flow separation behind the plankter, the

wake is thinner than the object moving through the water (see fig. 3D in Yen and Strickler, 1996). Not only is there minimal disturbance ahead of the copepod, but the smoothness of the trail indicates there is minimal disturbance within the wake. The Re estimated from these movements of the copepod and fluid is less than 10. Therefore, viscous forces dominate. What is the effect on signal structure and transmission? For the fluid-mechanical signal, viscosity attenuates flow. Within a few seconds, flows of millimeters per second quickly decay below the threshold levels of detection (Yen *et al.*, 1998). For the chemical signal, viscosity limits diffusion to molecular processes, and since molecular diffusion of a small chemical molecule is 1000 times slower than the dissipation of momentum (Table 1, Eqs. 4, 5), chemical signals are preserved. The signals appear as discrete trails and do not become diffuse plumes. The odorant is retained within the confines of the trail, with little mixing outside the trail. Molecular diffusive processes slowly expand the trail so that in 10 s, the signal is less than the threshold of a copepod's sensor (Yen *et al.*, 1998), implying that the copepod must find the trail within 10 s.

The structure of trail-like wakes has important consequences for copepods that use chemoreception to find their mates. The ability of the 1-mm copepod *Temora longicornis* to follow the trails of mates for up to 10 s after the trail was created confirms that, at the scale of this species, molecular diffusion acts to restrict the transport of the chemical so the trail persists until the male copepod finds it (Doall *et al.*, 1998; Weissburg *et al.*, 1998; Yen *et al.*, 1998). The observation that the male follows the trail precisely in three-dimensional space, indicating no change in odor structure, further confirms that eddy diffusion is minimal at these short (<10 s), small (<10 cm) scales. The copepod finds the trail because of the strong across-plume gradient, yet half the time he takes the trail direction away from the female because of a weak along-plume gradient (Doall *et al.*, 1998; Yen *et al.*, 1998). Analysis of the change over time in the location of the edge-detecting male, whose position is hypothesized to represent the location of the diffusing edge of the pheromonal trail, provides an estimate of $D = 2.7 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$, very close to the molecular diffusion coefficient of a small chemical molecule (Table 1, Eq. 5; Yen *et al.*, 1998). Observations of a male that lost the trail, at the moment when the female hopped, point to the importance of keeping the trail intact and not disrupting the signal. Because turbulence is known to elicit escapes and hops (Hwang *et al.*, 1994), it is important for copepods to reside in areas of low turbulence when mating signals are needed. When a male copepod loses the trail, he exhibits an isotropic search pattern. The minimal flow is not used for orientational guidance, as is essential to larger organisms in high Re flow (crabs, lobsters; Weissburg and Zimmer-Faust, 1993; Weissburg, 2000). The search is confined within a Kolmogorov-sized volume, suggestive of a strategy adapted

to life at the Kolmogorov scale, where water motion is limited by viscosity. Observations that copepods reside in layers of high Richardson's number (Gallager *et al.*, 1997) or low epsilon (ϵ ; Ince, 1996) also provide evidence of the importance of water stability to preserve these communication signals for successful mating and subsequent recruitment into the population.

Further analysis of the trails of *Temora* can give an indication of the type of eddy field wherein mate-tracking behavior can occur. The characteristic eddy turnover time T at size δ can be estimated as a function of the energy dissipation rate ϵ (Eq. 6, Table 1; Jiménez, 1997). In mating interactions of a copepod, the trail length could represent the eddy size, and the trail lifetime could represent the eddy turnover time. For *T. longicornis*, female trails are found within 10 s and can be tracked for 3.4 cm (Doall *et al.*, 1998; Weissburg *et al.*, 1998). If $\delta = 3.4$ cm and $T = 10$ s, then the upper limit of ϵ would be $1.16 \times 10^{-2} \text{ cm}^2 \text{ s}^{-3}$, a fairly energetic regime. These copepods come from Long Island Sound, a coastal semi-enclosed environment where turbulent mixing can be strong. Jiménez (1997) lists energy dissipation rates for coastal environments ranging from 10^{-3} to $100 \text{ cm}^2 \text{ s}^{-3}$. If this relationship in Equation 6, Table 1, is used to estimate ϵ from copepod behavior, it predicts that copepods with faster swimming speeds along the trail could live in areas of lower stability, whereas copepod trails that persist longer would indicate that the copepods are living in quiescent layers.

Vincent and Meneguzzi (1991) describe small-scale turbulence not as chaotic, but as having "organized structures", in which viscosity acts to correlate flow (Yamazaki, 1993). Coherent, correlated, and persistent physical features remain identifiable within the fluid motion of turbulent flows. One coherent small-scale turbulent structure is the vortex tube (Vincent and Meneguzzi, 1991). Yamazaki (1993) considers whether these structures help or hinder plankton interactions. Comparative analyses show many similarities in the structure of vortex tubes and copepod mating trails (see Table 2). The spatial aspect ratio and the temporal persistence of copepod trails and vortex tubes are remarkably similar (Table 2). Shear defines the boundaries of both features, yet the velocity gradients have slight differences. The shear intensity along a mating trail decreases downstream from the signal source, the swimming female copepod. Near the copepod, the shear gradient of the feeding/locomotory current is nonlinear, with an e-folding of 2.5 mm (falls by a factor $\exp(-1)$; Yen *et al.*, 1991), in contrast to the linear shear defining the edges of vortex tubes (Lazier and Mann, 1989). To ensure that the male has no trouble distinguishing his mate's trail from common vortex tubes, the female adds her phomonal chemicals.

Mating trails represent Kolmogorov scales. I propose the hypothesis that copepod behavior can be used as a measure of the Kolmogorov temporal and spatial scales (Table 2).

Table 2

Comparison of the properties of the biologically created copepod mating trail and those for the physically derived small-scale turbulent feature, a vortex tube

Mating trail	Kolmogorov scale
Isotropic (no directional flow)	Isotropic
Length = 5–10 cm	Millimeter to centimeter scale
Exploratory reach	Eddy size
10–50 mm long; 1–5 mm wide	10 : 1 aspect ratio
5–10 s	10 s persistence
Chemical pheromone: D = $10^{-5} \text{ cm}^2 \text{ s}^{-1}$	None*
Higher velocity gradient	Linear shear*

* Distinct.

The following observations, made on a few species of copepods in isolated experiments, led me to suggest this approach for the use of the copepod as a biosensor of the distribution of momentum and mass at Kolmogorov scales.

1. The volume searched and the isotropic search pattern inscribe a Kolmogorov eddy. The similarity in size and the lack of directional flow suggest that the male's behavior may be used as a measure of the Kolmogorov spatial scale.
2. The temporal change in the location of the odor-trail-edge-detecting copepod gave a diffusion coefficient similar to that for the molecular diffusion of a small chemical molecule. Here, the male's behavior provides a measure of the temporal scale.
3. The energy dissipation rate, estimated from eddy turnover time and eddy size for the mating trails, provides one estimate—based on copepod behavior—of the intensity of the local small-scale turbulence that closely matches known measurements of physical mixing in the copepod's local environment.
4. The similarity in (a) the response time of a copepod to the diffusing chemical trail and (b) the lifetime of a vortex tube suggests that copepods have evolved to create and respond to signals at the same time and length scales as small-scale turbulence.

These observations for the copepod species *Temora longicornis* (Doall *et al.*, 1998; Weissburg *et al.*, 1998; Yen *et al.*, 1998) suggest that it has adapted to the limitations imposed by the physical environment. This copepod constructs communication signals and enacts behavior within the constraints of transitional Re realms. Analysis of similar behavior of other copepods may provide us with representations of the temporal and spatial measures of Kolmogorov scales of fluid physical motion.

Escaping

As mentioned in the introduction, routine swimming and feeding take place in low Re regimes and laminar fields, whereas escapes and captures occur at high Re realms in quasi-turbulent fields. During escapes, vortices and toroids are shed (Yen and Strickler, 1996). To achieve the power needed to move at escape speeds that can reach up to 1 m s^{-1} (Fields, 1996), the copepod executes a series of jumps that rely on its larger swimming legs rather than on the small cephalic appendages that are used for generating the feeding current or for travel *via* laminar cruising. During the recovery stroke of swimming legs in a jump, the oar-like rami are feathered so they form a median longitudinal keel (Boxshall, 1985). During the escape, the antennules are folded against the body sides with legs flattened against the urosome and the caudal rami folded shut like a closed fan (Fig. 1). Analyses of high-speed jumps show that jets are formed when the swimming legs collapse against the urosome during escape maneuvers (Strickler *et al.*, 1995; Liu, 1996). Examination of the copepod skeletal system reveals the design features for maximum efficiency in the jump (Boxshall, 1985). The prosome-urosome joint in copepods has a transverse pivot line with extensive arthroal membrane (thinner than the cuticle) dorsally and ventrally that permits considerable dorsoventral, but little lateral, flexion. The evolution of the prosome with its complex ventral wall lacking articulation between somites appears to have been closely linked to the perfection of the jumping mode of locomotion. Manton (1977) stated that "the whole skeletal system concerned with the copepod's jump is of such strength as to prevent unwanted flexure which might detract from the force of the jump." Contraction of the dorsal longitudinal musculature, which fans out laterally in the urosome to a broad dorsal-to-lateral insertion inside the anal somite (Boxshall, 1985), may act to close the fan-like caudal rami into a narrow tail, telescoping somites within the preceding one.

Not only is the skeletal system designed for maximum efficiency, but the resultant body form further allows copepods to attain and maintain maximum observed escape speeds of 1 m s^{-1} (Fields and Yen, 1997) to enter into the inertial realm of $Re = 1000$. When executing an escape, the copepod adopts a profound change in morphology—from an expanded form to a smooth streamlined shape (Fig. 1). In the expanded non-escape posture, the horizontal caudal fan may be important in controlling the pitch, or attitude, of the copepods and also may act as a stabilizer in reducing roll about the longitudinal axis (Strickler, 1975). In the streamlined form, the copepod may spiral around its central long axis (pers. obs.). In this escape posture, streamlining changes the pressure field behind the copepod where the fluid gradually decelerates in the rear, little or no separation occurs, and the object is literally pushed forward by the



Figure 1. Escape postures of *Euchaeta rimana* adult female (prosome length = 2.4 mm). (Top) Streamlined body form during escape glide of copepod moving at Reynolds numbers greater than 500, showing antennules parallel to body, swimming legs folded close to body, and caudal rami collapsed into a narrow tail. (Middle) Body form during power thrust of the escape, showing antennules folded parallel to body and exopods of the swimming legs extended and caudal rami flared. (Bottom) Body form when swimming and hovering prior to escape, with antennules positioned at right angles to body. The panels were placed in this spatial order to depict how the body form changes in the direction of an upward escape.

wedgelike closure of the fluid behind it (Vogel, 1994). The gain from adopting a streamlined morphology, effective at high Re , implies that, indeed, copepods do operate within an

inertial realm. The necessity for an effective escape from predators has driven the evolution of the streamlined form of copepods.

When a large copepod escapes, toroidal vortices are found in its wake as larger appendages translate larger parcels of water (Fig. 2). A toroidal shape can be viewed as a vortex ring due to the vorticity produced by viscosity between the jet and the ambient fluid (Weihs, 1977). A toroidal vortex gets larger by entrainment of surrounding fluid and slower by loss of its original impulse (Shariff and Leonard, 1992; as cited by Vogel, 1994). Analyses of the change in volume and distance traveled by the toroidal vortex allow an estimate of the relative importance of diffusive to advective forces within this copepod wake. Here, 250 ms after the copepod has released the torus, the torus continued to grow by 20% over the past 50 ms (see Fig. 3; Table 3). The water continues to coast 0.4 s after the source has left the scene, further evidence of entrance into an inertial realm. In fact, it takes another 2 s before the Peclet number approaches 1 and advection is balanced by diffusion (from Table 1, Eq. 2, $Pe = 1$ when $U = 1 \mu\text{m s}^{-1}$; from Table 3, Eq. 3, $t = 2.55 \text{ s}$ for $U = 1 \mu\text{m s}^{-1}$). Since these wakes were visualized within a strong density gradient, they may be smaller and slower than natural wakes formed in an ambient density gradient (see Gries *et al.*, 1999) and may inaccurately estimate the time needed to reach a balance between advection and diffusion. During this time, odor placed within the torus is dispersed by advection. A signal of mixed modality is created when the concentrated odor of excreted metabolites is encased in the jet-like wake shed by an escaping copepod. The concentration of odorant in the wake will be more dilute than that in the laminar trail because viscous forces do not restrict the advective disruption of odors *within* the wake of a swimming copepod. This rapid odorant dilution may be more difficult to follow if a chemosensory predator chases the copepod prey. The energetic hydromechanical signal also may frighten predators because of the apparent large size and strength, a form of aposematism. It also may act as a decoy, since the source is distant from the signal. When in proximity to the source, the hydromechanical signal has directional information that guides the male copepod when he executes the final capture of his mate at the end of the pheromonal trail (Yen *et al.*, 1998).

The odorant distribution within the torus also is not the same as expected from diffusion. According to Okubo (1984), "an essential difference between the mechanisms of molecular and turbulent diffusion exists, where the flux of a property by molecular diffusion takes place always from the higher concentration to the lower concentration and is proportional to the concentration gradient. Turbulent flux, however, need not always be in the direction of down-gradient of the mean concentration nor can it always be described as diffusion." Close examination of the Schlieren image,



Figure 2. Dynamic analysis of figure 3A in Yen and Strickler (1996) showing the sequence of toroid structures separated by 67 ms. Note the lack of change in the location of the initiation point of the toroid, the advective movement of the head of the hydrodynamic feature, the vortices formed as the water moves, the growth of the toroid over 333 ms, and the fine-scale patchiness in color intensity (which can correspond to chemical concentration: for methods, see Strickler *et al.*, 1995). Scale bar = 4 mm.

where the brightness of the signal can be representative of the concentration gradient (Strickler *et al.*, 1995), shows

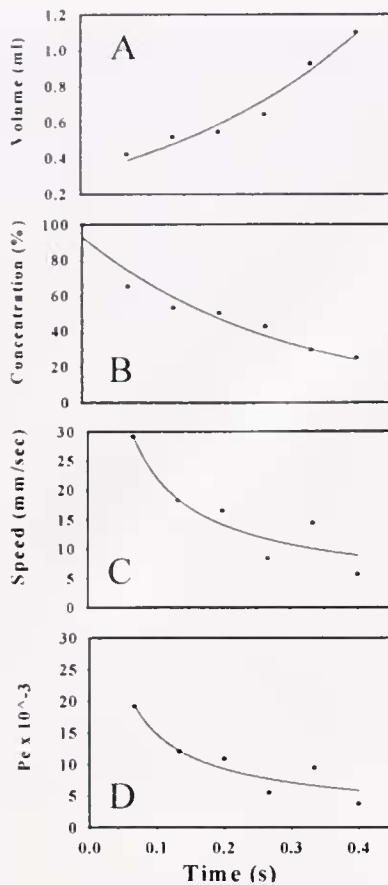


Figure 3. Dynamics of toroid growth in the wake of an escaping copepod. The rightmost full toroid in Figure 2 is analyzed here. (A) Increase in the volume of the toroid. Volume was determined by estimating the chord length of the toroid and the average width and calculating the volume using the formula for a cylinder. The values were fit with a sigmoid equation (see Table 2). (B) Decrease in concentration of a hypothetical odorant, presuming the initial concentration is 100%. Data were fit with a two-parameter exponential decay curve. (C) Decline in the speed of the toroid as it moves away from the location where it was created by the copepod. Data were fit with a two-parameter exponential decay curve. (D) Decline in Peclet number showing a strong influence of advective forces over a period of seconds. Data were fit with a one-parameter power function. Fitted equations appear in Table 3.

how the biological activity of copepod eddies contributes to the rates of change of tracer microstructures. Figure 2 shows separate vortices created by the intermittent jets of an escaping copepod, expanding in volume, driven by the momentum imparted by the escaping organism. In this type of eddy packaging, odor is not dispersed along a diffusive gradient and can be observed patchily distributed in a spatial pattern characteristic of the advective movement within the vortex. Analysis of the microstructure shows that the signal is dispersed unevenly within the advective feature yet the boundaries still are delineated by the encroachment of viscous fluid. As described by Gries *et al.*, (1999), the physical structure of the wake constrains the patchy distribution of nutrients released by the zooplankton. Copepods may follow the patchy odor distribution within a toroid with a less directed routing than when following a laminar trail. Copepods do respond to different structures with different behaviors. For example, when a slowly advancing hovering copepod created a diffuse wake below her, the mate-tracking male was found to cast within the wake in a zigzag fashion. This behavior was very different from the tracking of the exact three-dimensional trail of a male following a cruising female (Doall *et al.*, 1998; Weissburg *et al.*, 1998). The male took a longer time to zigzag within a diffuse trail than to quickly follow the thin trail left by a cruising female copepod (Weissburg *et al.*, 1998). The combined information from the flow signal and patchy odor signal influences the mechanisms that guide the plankter to the source.

Signaling is affected by the balance of viscous and inertial forces. Copepods take advantage of the transition between laminar and incipient turbulent flow to maximize the efficiency of movements. They modify their morphology and speed of movement to conform to the laws of fluid physics. The escaping copepod is much more streamlined than the sinking or slow-swimming copepod with all its sensors deployed. These differences affect the signals generated in the various copepod gaits. The slow swimming of the low-drag, minimal-surface-area oblate spheroid form of the nauplius leaves little trace of its presence or passage. The cruising of the adult copepod leaves a coherent laminar trail with a strong chemical signal but a weak fluid-mechanical signal. The high speed of the streamlined escaping

Table 3

Dynamics of toroid formation by escaping copepods (see legend for Figure 3)

	TOROID 2 (at $t = 0.067$ s; at $t = 0.4$ s)	TOROID 3 (at $t = 0.067$ s; at $t = 0.4$ s)	Fitted equation	R ²
Copepod speed (cm s ⁻¹)	38 (initial)	30 (initial)		
Toroid volume (ml)	0.2; 1.2	0.2; 1.2	$V = 35.9/(1 + e^{(t - 0.067)/0.12})$	0.965 (1)
Concentration (% original)	100; 20	100; 20	$C = 93e^{-3.4t}$	0.948 (2)
Toroid speed (mm s ⁻¹)	38; 4.1	30; 5.7	$v = 36.58e^{-4.2t}$	0.848 (3)
Peclet number	28,000; 3,075	19,000; 3,750	$Pc = 3180t^{-0.67}$	0.868 (4)

copepod leaves energetic jets that contain strong fluid-mechanical signals retaining chemical signals within the borders.

A consequence of movement through transitional fluid regimes is that the relative strength of the chemical and fluid-mechanical signals changes: the fluid-mechanical signal increases in importance at high Re within the range experienced by copepods. Responding to the input from the shift in sensory modalities and the difference in the dissipation rate of momentum which is 1000 times faster than the diffusion rate of mass (Table 1, Eqs. 4, 5), copepods adjust their behavioral responses to suit this transition in the mixture of fluid-mechanical and chemical signals. Fast responses resulting in predator avoidance or carnivory tend to be elicited by short-lived fluid-mechanical signals, whereas slow responses resulting in grazing, swarming, and mate-tracking tend to be elicited by persistent chemical signals. The careful diversion to the mouth of the alga-carrying odor-laden streamline in the feeding current and the exact mate-tracking elicited by chemical signals as well as the accurate prey-attacks and oriented escapes elicited by fluid-mechanical signals exemplify the precision maintained in the directed response of copepods to water-borne signals. Analysis of the chemical paths followed or the locations of escape from shear may provide additional behavioral indicators of the distribution of mass or momentum.

Ecological Consequences of Small-Scale Biological-Physical-Chemical Interactions

Encounter probabilities

In 1995, Haury and Yamazaki examined the length scale at which the shift occurs between biologically controlled (growth rate, swimming ability, perception distance) and physically controlled (e.g., turbulence, vertical current shear) distributions of zooplankton. They found a dichotomy in the magnitude of the discrepancy between the known perception distances of planktonic organisms and nearest-neighbor distances (NND) between conspecifics measured within patches. "The discrepancy suggests that (i) the signals used to maintain aggregations are not yet identified, and/or (ii) copepods are more sensitive to known signals than we can measure or explain theoretically." Our studies of mating interactions address both of these suggestions. The documentation of chemical mating trails and the sensitivity of copepods to the Kolmogorov-scale distribution of momentum and mass changed the measure of reactive distance, a key parameter in plankton encounter models. We found that mate-tracking copepods can be separated by straight-line reaction distances of up to 3.4 cm where male copepods follow curved trails up to 6.5 cm long with pursuit distances of up to 13.8 cm (pursuit distances can be longer than the trail when the copepod backtracks; Doall *et al.*, 1998). These studies have increased our measure of

reaction distances by 10- to 100-fold from the one-to-two-bodylength (<5 mm) reaction distances of copepods to algal or animal prey. Nearest-neighbor distances of commonly found swarm densities (1–5 cm in patches of 10^4 to 10^6 copepods m^{-3} ; Haury and Yamazaki, 1995) are now comparable to reactive distances, making sense of the significance of patchiness. Plankton can rely on local thin layers and patches as areas of intense activity and high encounter probabilities in which survival strategies can be completed. By migrating to layers where the persistence of communication signals is maximized or most amplified, copepods can aggregate at the pycnocline to reduce NND and enhance encounter probabilities.

Encounter probability can be improved not only by larger perceptive radii and swarming but also by changes in speed and swimming directionality, and copepods engage in these modifications. Rapid chemo-orientation in response to female trails allows the male copepod to catch up to his mate. In contrast to the three-dimensional isotropic trails of *Temora*, *Calanus* females leave vertical trails, and the male performs a search dance primarily in the horizontal plane (Tsuda and Miller, 1998). Perpendicular swimming patterns, which improve the efficiency of encounter (Gerritsen, 1980), also have been documented for male and female *Euchaeta* (Yen, 1988). Hence, discoveries in the micromechanics of mate detection have improved our understanding of encounter probabilities within patches and, as a consequence of increased encounter rates between mates, larger scale population dynamics will be enhanced by the improved likelihood of reproductive success.

Spatial sorting

In spatial sorting, the distribution of copepod populations results in an apparent match between the intensity of the physical forces and the intensity of various biological functions (such as making feeding currents or escaping). Comparison of the feeding currents of copepods from energetically different environments (Fields, 1996; Fields and Yen, 1996) shows a correlation between the flow speed and the strength of physical mixing: copepods are found in ocean layers in which Kolmogorov flow speeds are similar to the feeding current flow speed. Spatial sorting may be occurring to minimize the expenditure needed to maintain the feeding current that is a requisite for gathering chemical signals. The sensitivity of copepods to a threshold level of shear appears to be related to the energy level of their environment, higher levels of shear are necessary to elicit escapes from coastal copepods, while lower intensities elicit responses from open-ocean copepods (Fields and Yen, 1997). This suggests that these organisms have adapted their sensory systems or have been sorted spatially to zones where the shear levels are less than their behavioral threshold signal strength, minimizing energy loss to unreasonable responses. The

discovery of the persistence of mating trails, necessary for the essential survival tactics of reproduction and the perpetuation of the species, further suggests that, to preserve mating signals, copepods may seek regions where turbulent eddy diffusion is minimal and stability is high. Indeed, Mackas *et al.* (1993), Mackas and Miller (1990), and Ineze (1996) found copepods vertically distributed according to ε . Haury *et al.* (1990) found that after a storm, zooplankton are selectively mixed to a distribution different from their vertical separation under less energetic conditions. To ensure the efficiency of mate-finding, copepods may avoid areas of high turbulence where flow patterns elicit escapes (Hwang *et al.*, 1994); the escape wakes disperse the odor trail, creating an intermittent signal that cannot be followed. The fact that, without mating, no future generations are supported attests to the strength of the evolutionary pressures on copepods to reside in an oceanic zone where the strength of the biological signal and the sensitivity of the organism closely match the physical energy of the fluid environment.

Concluding Remarks

In 1988, Yamazaki and Osborn asked: "How are creatures affected by the mean and fluctuating portions of the circulation? Have they responded to the temporal and spatial distribution of turbulence? Are they adapted to the 'variability of the ocean' rather than the 'mean'?" Analyses of copepod behavior show responses to both scales of fluid motion. The timing of the life history of eel larvae to transit times of the Sargasso Sea gyre (Harden Jones, 1968) and the timing of the vertical migration of estuarine plankters to the direction of tidal excursions (Cronin, 1982; Forward and Rittschof, 1994) show adaptations to the mean flow. In this study, copepod behavior reveals adaptations to the fluctuating component of ocean flow. Avoidance of rogue waves of small-scale turbulence is required for mating success, but living in an ocean layer with similar biological and physical ε is fine for feeding success since the feeding current can be rebuilt. The physically derived fluid motion can enforce the zonation of copepod species to ocean layers in which the environmental turbulence is similar to the strength of the biologically created flow and to copepod sensitivity.

In 1984, Strickler stated that "Viscosity acts as a selective force in the evolution of copepods" and "copepods take advantage of [this]." In 1993, Yamazaki commented, "Zooplankton have evolved behavioral adaptations to flow patterns." Recent results indicate that not only is viscosity an important force but so are inertial forces. Inertial forces distribute the odorant within the wake and convey information about the size and speed of the propagator. Viscous forces act to restrict chemical diffusion within the hydrodynamic borders and attenuate the flow signal within seconds and millimeters. Suitable responses to these variations in the spatial distribution and temporal persistence of chemical

and fluid-mechanical signals contribute to the success of copepods in the sea. Perceptive volumes, signals, and response times similar to the length and time scales of small-scale turbulent features suggest that copepods are adapted to the physical constraints of Kolmogorov scales. Within the whorl of a copepod, biological and physical forces are in a fair competition for dominance. At these small scales, copepods can conform or deform the physical environment for their survival, using morphological and behavioral adaptations to shift the balance in their favor.

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